

ASSESSING TIGER POPULATION DYNAMICS USING PHOTOGRAPHIC CAPTURE–RECAPTURE SAMPLING

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Abstract. Although wide-ranging, elusive, large carnivore species, such as the tiger, are of scientific and conservation interest, rigorous inferences about their population dynamics are scarce because of methodological problems of sampling populations at the required spatial and temporal scales. We report the application of a rigorous, noninvasive method for assessing tiger population dynamics to test model-based predictions about population viability. We obtained photographic capture histories for 74 individual tigers during a nine-year study involving 5725 trap-nights of effort. These data were modeled under a likelihood-based, “robust design” capture–recapture analytic framework. We explicitly modeled and estimated ecological parameters such as time-specific abundance, density, survival, recruitment, temporary emigration, and transience, using models that incorporated effects of factors such as individual heterogeneity, trap-response, and time on probabilities of photo-capturing tigers. The model estimated a random temporary emigration parameter of $\hat{\gamma}'' = \hat{\gamma}' = 0.10 \pm 0.069$ (values are estimated mean \pm SE). When scaled to an annual basis, tiger survival rates were estimated at $\hat{S} = 0.77 \pm 0.051$, and the estimated probability that a newly caught animal was a transient was $\hat{\tau} = 0.18 \pm 0.11$. During the period when the sampled area was of constant size, the estimated population size \hat{N}_t varied from 17 ± 1.7 to 31 ± 2.1 tigers, with a geometric mean rate of annual population change estimated as $\hat{\lambda} = 1.03 \pm 0.020$, representing a 3% annual increase. The estimated recruitment of new animals, \hat{B}_t , varied from 0 ± 3.0 to 14 ± 2.9 tigers. Population density estimates, \hat{D}_t , ranged from 7.33 ± 0.8 tigers/100 km² to 21.73 ± 1.7 tigers/100 km² during the study. Thus, despite substantial annual losses and temporal variation in recruitment, the tiger density remained at relatively high levels in Nagarahole. Our results are consistent with the hypothesis that protected wild tiger populations can remain healthy despite heavy mortalities because of their inherently high reproductive potential. The ability to model the entire photographic capture history data set and incorporate reduced-parameter models led to estimates of mean annual population change that were sufficiently precise to be useful. This efficient, noninvasive sampling approach can be used to rigorously investigate the population dynamics of tigers and other elusive, rare, wide-ranging animal species in which individuals can be identified from photographs or other means.

Key words: camera-trapping; capture–recapture; carnivores; demographic parameters; elusive species; macroecology; noninvasive surveys; *Panthera tigris*; population modeling; robust design; tigers; trend estimation.

INTRODUCTION AND OBJECTIVES

Populations of many large, wide-ranging carnivore species are threatened because of anthropogenic pressures that come into conflict with their basic ecological needs (Woodroffe and Ginsberg 1998, Treves and Karanth 2003). However, strong inferences about population dynamics of such carnivores, while useful for their conservation, are scarce because of numerous problems involved in conducting rigorous studies at the required spatial and temporal scales. Here we present results of a study of population dynamics of the tiger (*Panthera tigris* Linn.; see Plate 1), a highly endangered,

large carnivore species of global concern that typifies the challenges involved in studying large, wide-ranging, rare, or elusive carnivores.

Despite three decades of substantial conservation efforts (Seidensticker et al. 1999), tigers continue to suffer range contractions through continuing extirpation of local populations. A widely prevalent perception attributes this decline of tigers to illegal killing for trade in their body parts. However, using field studies of predation (Karanth and Sunquist 1995, 2000), Karanth and Stith (1999) developed a demographic model indicating that decline of tiger populations is primarily a consequence of prey depletion rather than direct killing because of their high reproductive potential in prey-rich habitats. This model is also supported by more recent data from field studies showing strong dependence of tiger density on prey abundance (Karanth et al.

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2004). However, testing the prediction based on this model, that tiger populations within prey-rich protected reserves are demographically viable in spite of high rates of annual loss, requires estimation of tiger abundance and vital rates at large spatial and temporal scales.

Two key problems of animal population sampling are the inability to survey the entire area of interest and the inability to detect all individuals even within the surveyed area (Williams et al. 2002). These problems have proven to be particularly intractable when estimating abundances and vital rates of rare or elusive species (Thompson 2004). Such problems are exemplified by the tiger, which has an extensive range spanning a 1.5 million km² area across Asia, within which surviving populations occur patchily and at low densities. Thus far only two studies, in Nepal (Sunquist 1981, Smith 1993, Kenny et al. 1995) and Russia (Kerley et al. 2003), respectively, both involving radio tracking of 30–40 individuals, have generated some ad hoc estimates of tiger survival rates. However, high costs and logistical difficulties severely limit the potential use of radiotelemetry for estimating demographic parameters in tiger populations.

In recent years, relevant methods of population analysis (Seber 1982, Burnham and Anderson 2002, Williams et al. 2002) have advanced greatly, permitting investigators to handle both biological and statistical complexities involved in sampling populations of wide-ranging, rare, and elusive species (Thompson 2004). Benefiting from these advances, Karanth (1995) showed that “photographic captures” of tigers obtained from automated “camera traps” could be analyzed under a closed-population capture–recapture sampling framework (Otis et al. 1978, White et al. 1982, Chao and Huggins 2005). These methods have been refined subsequently (Karanth and Nichols 1998, Karanth et al. 2002, Nichols and Karanth 2002). Since then, photographic capture–recapture sampling has been successfully employed to estimate tiger abundances at several sites across Asia (O’Brien et al. 2003, Karanth et al. 2004, Kawanishi and Sunquist 2004, Wegge et al. 2004). However, such efforts have been restricted to single-season studies that provide “snapshots” in time, permitting inferences only about spatial variation in tiger abundance (e.g., Karanth et al. 2004), but not about temporal dynamics.

Estimates of a state variable such as tiger abundance (or density) obtained from a single location over multiple years can yield estimates of rates of population change. Photographic capture histories of individual animals over years also permit estimation of the vital rates (survival, recruitment, movement) that actually drive such changes in abundance (e.g., Williams et al. 2002). These estimates can be used to test model-based predictions, such as those of Karanth and Stith (1999), to gain a more complete understanding of tiger population dynamics as a basis for future management.

In this study, we extended camera-trap sampling temporally to obtain capture history data for individual tigers over multiple seasons at a single location using the “robust design” capture–recapture approach (Pollock 1982, Pollock et al. 1990, Kendall et al. 1995). This capture–recapture design includes several secondary sampling occasions within each primary period (each season or year). The capture histories obtained are used to estimate parameters such as time-specific abundance, annual survival rate, and number of new recruits. This approach explicitly models the effect of capture probabilities on capture history data and is more efficient in terms of costs and effort than any other proven method of sampling tiger populations (Karanth et al. 2002, Nichols and Karanth 2002).

Efficiency can be further increased over that of single-season studies by the possibility of using reduced-parameter models in which certain parameters are constant over time (Lebreton et al. 1992). Such modeling effectively borrows information from multiple years to obtain more precise estimates of quantities of interest (e.g., tiger density) for any particular year (MacKenzie et al. 2005). Of course, there is always some danger of bias associated with reduced-parameter models, and we follow the recommendations of Burnham and Anderson (2002) and use model selection approaches designed to provide optimal solutions to the problem of finding parsimonious models.

Some investigators considering methodology for estimating trends in tiger abundance over large areas of India have emphasized the relative imprecision of single-year abundance estimates, suggesting that it would be impossible to obtain relatively precise estimates of trend using camera-trap data. However, we believe that the opportunities for reduced-parameter modeling and effectively borrowing information over time under the robust design are likely to improve the precision of estimates of population change substantially.

Our study was conducted in the central part of Nagarhole reserve in Karnataka State, India, from 1991 to 2000 (Fig. 1; See Karanth and Nichols [1998] for site details). This 644-km² reserve supports high densities of prey (~56 ungulates/km²) and, consequently, of tigers (Karanth and Nichols 1998, Karanth et al. 2004). The tiger and associated prey populations within the sampled area were reasonably well protected. The surrounding landscape matrix, consisting of other protected areas, multiple-use forests, and agricultural land, provided some possibilities for tigers to move in and out of the study area (Fig. 1).

These conditions led us to predict that the Nagarhole tiger population should be relatively stable despite heavy annual losses from mortalities and dispersal. Given the nature of the surrounding landscape, consisting of high-productivity reserves embedded in a multiple-use landscape matrix hostile to tigers, we also expected a relatively high proportion of transient tigers in search

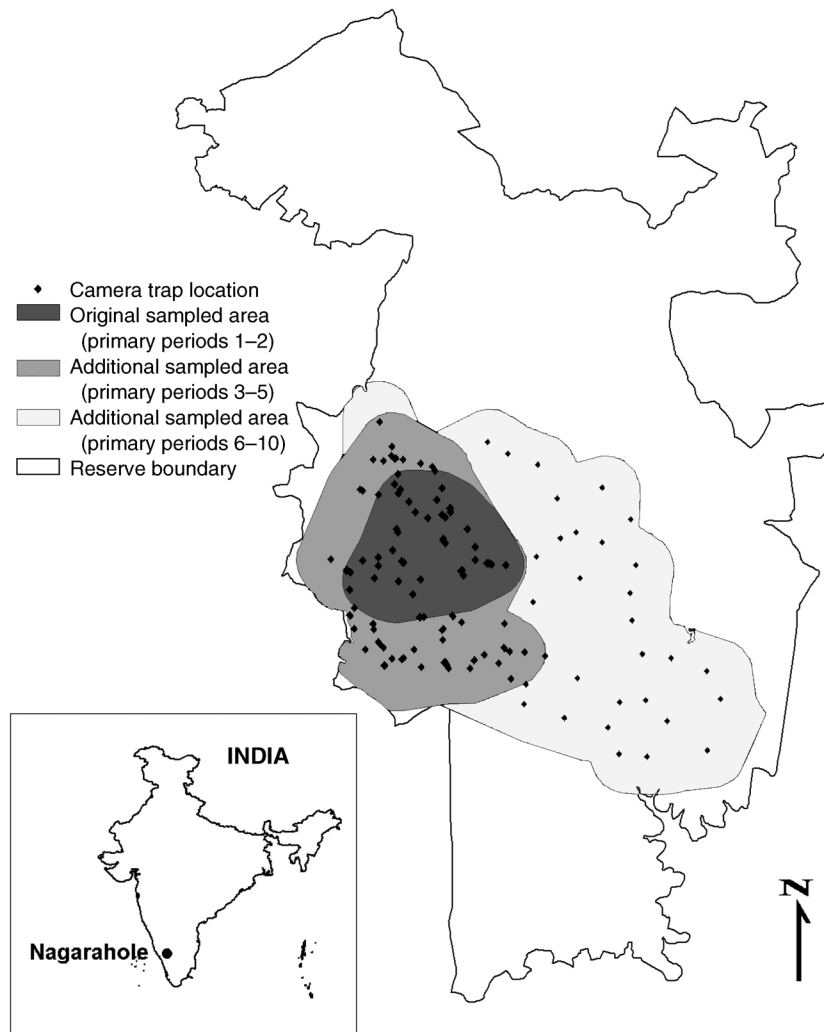


FIG. 1. Map of the areas sampled by camera traps in Nagarahole during 1991–2000. The inset shows the location of the study site within India.

of territories. In order to test these hypotheses, we had to estimate time-specific tiger abundance, survival, transience, and other relevant parameters for the Nagarahole tiger population. Therefore, a related specific objective was to design and field-test a robust design capture–recapture sampling protocol using camera traps to sample tiger populations across large spatial and temporal scales. We hoped to develop models that would estimate quantities of interest while properly accounting for aspects of tiger behavior and movement patterns that are likely to affect sampling. Specifically, we wanted to use camera-trap-derived photographic capture histories, in conjunction with models that permitted transience, temporary emigration, and variation in probabilities of initial capture and recapture among individual animals, to estimate tiger abundances, densities, annual survival rates, numbers of new recruits, and rates of population change over time. Despite the relative imprecision of single-season abundance esti-

mates, we hoped that modeling of multiple years of data would yield relatively precise estimates of population change. Finally, we wanted to consider the ecological and conservation implications of our results for understanding the population dynamics of tigers and other similar rare and elusive species.

METHODS

Field methods

We captured tigers using camera traps that simultaneously photographed both flanks from a distance of 3.5 m using an active infrared tripping mechanism. The camera traps were placed at optimal locations, based on presence of tiger signs, to simultaneously maximize capture probabilities while sampling the entire area of interest (leaving no “holes” in which tigers could have near-zero probabilities of detection). Details of equipment and survey protocols have been fully described

TABLE 1. Primary and secondary sampling periods, sampled areas, camera-trapping effort, and number of individual tigers photo-captured at Nagarahole, India, 1991–2000.

Primary period	No. secondary periods	Mid-point	No. days	Area sampled† (km ²)	Effort trap-nights	No. tigers caught	Cumulative no. tigers caught
1	6	May 1991	162	41.4 (3.3)	294	9	9
2	5	Dec 1991	127	41.4 (3.3)	87	4	10
3	3	Apr 1992	75	101.5 (5.2)	108	5	13
4	7	Jan 1994	197	101.5 (5.2)	668	17	24
5	10	Jan 1995	78	101.5 (5.2)	691	12	26
6	18	Mar 1996	118	231.8 (7.8)	938	26	44
7	8	Jun 1997	33	231.8 (7.8)	448	15	47
8	12	Jan 1998	39	231.8 (7.8)	695	16	50
9	15	Mar 1999	47	231.8 (7.8)	868	22	60
10	15	May 2000	54	231.8 (7.8)	928	28	74

† The estimated mean sampled area \bar{A} and its estimated standard error (in parentheses) were calculated as described in Karanth and Nichols (1998).

elsewhere (Karanth and Nichols 1998, Karanth et al. 2002). Because of the limited number of camera traps available, we initially sampled only a 41.4-km² area. With increased availability of traps, we expanded the sampled area, successively, to 101.5 km² and to 231.8 km². Thereafter, the sampled area remained constant (Fig. 1, Table 1). We invested a total sampling effort of 5725 camera-trap-nights that resulted in photographic captures of 74 individual tigers during the nine-year study (Table 1). The differences in stripe patterns were sufficiently distinct to permit unambiguous identification of individual tigers (Fig. 2).

Analytic methods

This field-sampling protocol yielded capture histories of individual tigers in the standard X -matrix format (Otis et al. 1978). Following standard capture–recapture terminology for the “Robust Design” (Pollock 1982, Kendall et al. 1995, 1997, Williams et al. 2002), this study consisted of 10 “primary periods” or seasons of sampling covering nine years. The tiger population was expected to be open to gains and losses between these primary periods. There were multiple “secondary sampling periods” within each primary period, and the population was assumed to be closed to gains and losses among these secondary periods, an assumption that we tested.

Our analytic methods dealt with possible effects of individual heterogeneity, trap-response behavior, and time-related variations on capture probabilities (Otis et al. 1978, Williams et al. 2002). Given prior knowledge about tiger movements and social organization patterns (Sunquist 1981, Smith 1993, Smith et al. 1999, Karanth and Sunquist 2000), we tried to realistically model temporary emigration (the probability of an individual tiger not being available for trapping during one or more primary sampling period); transience (the probability that a newly captured individual tiger was just passing through the study area, with a near-zero chance of returning to be recaptured during the study); and losses (the probability of death or permanent emigration).

Although we estimated tiger abundance for all primary periods, it was biologically meaningful to estimate change in abundance only for periods 6–10 when the sampled area was constant. We estimated numbers of recruits and rates of change in tiger abundance only for this period, because estimates for the earlier period would reflect changes in study area as well as tiger population dynamics.

Survival estimation was hypothesized to be unaffected by these increases in study area, and we tested this hypothesis by assessing the utility of models with time-dependent survival vs. models with time-invariant survival. All analyses excluded cubs because of their low photo-capture probabilities (Karanth and Nichols 1998, Karanth et al. 2004), and grouped all tigers into a single demographic class because of relatively small sample sizes (Table 1).

Pollock’s (1982) original recommendation for the robust design was as a two-stage analysis. Abundance was to be estimated using closed-population models with capture history data across secondary periods within each primary period. Survival was then to be estimated by combining data across secondary periods to indicate whether or not an animal had been caught at least once during a primary period, and then analyzing the resulting capture histories using open models across all primary periods. Kendall et al. (1995, 1997) then developed full likelihood approaches that combined these two kinds of models within a single analysis.

In our analysis of tiger data, we initially followed the original two-step approach in a set of preliminary analyses in order to gain insight into how to best model the combined data set. We then used this insight to develop a set of models for use with the entire data set. This two-step approach is an attempt to reduce to a manageable number of models in the set for the final analysis. This approach is similar to that of other large analyses (e.g., Franklin et al. 2004) of first modeling capture probability and then conditioning on a selected model for this parameter and modeling the other parameters of interest (e.g., survival).

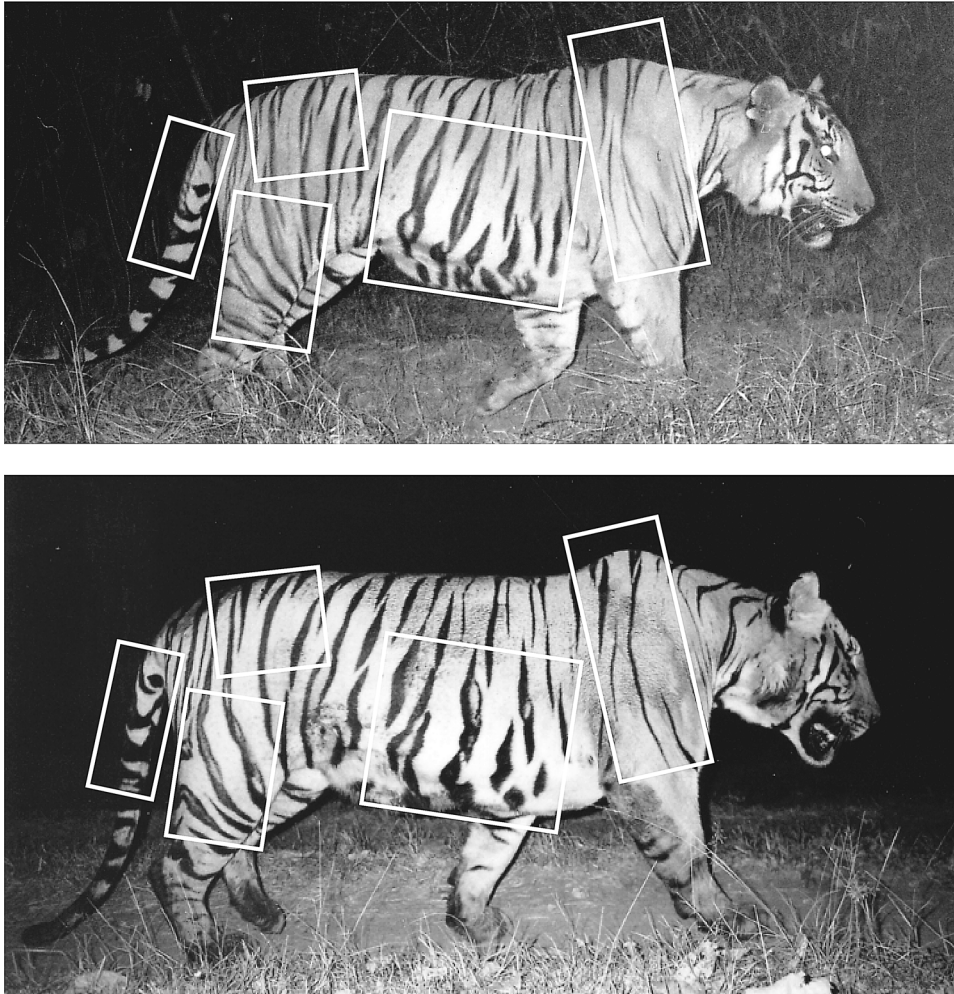


FIG. 2. Photographs of two different tigers obtained by camera traps in Nagarahole, India, showing differences in stripe patterns that permit unambiguous identification of individuals.

Initially, we conducted analyses and tests of population closure on capture data from each primary period separately, using program CAPTURE (Otis et al. 1978, Rextad and Burnham 1991). The closure test of CAPTURE is based on the time between first and last captures, and we report the associated z statistics. We also investigated the modeling of capture probabilities by assessing the discriminant function model selection statistics for the four likely models (Otis et al. 1978) for tiger data: M_0 (constant capture probability), M_h (capture probability heterogeneous among individuals), M_{bh} (behavioral response in capture probability with heterogeneity among individuals), and M_{tbh} (capture probability affected by secondary sampling period, trap response, and heterogeneity).

Secondary capture history data within each primary period were then collapsed to form an open-model capture history indicating whether an animal had been detected at least once or not during a primary period. These data were subjected to goodness-of-fit tests

(Pollock et al. 1985, Burnham et al. 1987) using program RELEASE. In addition to the general goodness-of-fit test, the test component TEST3.SR provides inference about the existence of “transience” manifested by different subsequent survival probabilities for animals that are previously captured vs. animals captured for the first time. TEST3.SR provided some evidence of a difference (see *Results*), so model selection was used with software TMSURVIV (Pradel et al. 1997) to assess the need for “transient models” in which animals caught for the first time are viewed as comprising a mixture of resident animals and animals that are transients, which have near-zero probability of being recaptured at a later time.

Results of these various closed-population and open-population analyses led to the development of a set of 30 models for the entire robust design data set. The capture data for secondary sampling periods within each primary period were modeled using closed-population model components that did not include time (secondary

periods), but did include heterogeneity and behavioral response in capture probability. Heterogeneity was modeled using a finite mixture model (Norris and Pollock 1996, Pledger 2000) with two groups of animals. A transient parameterization was used for the survival portion of the modeling, with a focus on models that did not include time (primary periods), as indicated by the open-population modeling. Finally, the combined model included temporary emigration parameters to admit the possibility that some animals in the superpopulation (animals in the general vicinity of the area exposed to sampling efforts, although not necessarily within the sampled area during each primary period) were absent and not exposed to sampling efforts during some periods (Kendall et al. 1997, Williams et al. 2002). All of these models were implemented in program MARK (White and Burnham 1999).

The set of models for the combined robust-design data included a number of parameters. Abundance (number of tigers in the sampled area) was always modeled as time dependent, resulting in one parameter for each primary sampling occasion, denoted as $N(t)$ in our model notation. Survival is expressed on an annual scale, even though the times separating adjacent primary sampling periods were seldom exactly one year. Annual survival was generally modeled as not varying over time, based on open-model results, and was either modeled as the same for all animals, $S(\cdot)$, or as differing between animals caught for the first time in the study and recaptured animals, $S(a)$. We also included a $S(a + t)$ model, in which new and recaptured animals showed different survival rates that varied in parallel (on a logit scale) over time, and a $S(a, t)$ model in which survival for new animals was a constant and survival for previously caught animals varied over time. The probability of being a temporary emigrant was modeled as either different depending on whether the animal was (γ') or was not (γ'') a temporary emigrant the previous period, or not, $\gamma' = \gamma''$. In addition, these temporary emigration parameters were either time dependent, $\gamma'(t)$, or not, $\gamma'(\cdot)$.

The notation for capture probability included an initial parameter, π , when heterogeneity was included in the model. This is the mixing parameter of the Pledger (2000) finite mixture models and simply indicates the proportion of the population in one of the two groups of individuals. The proportion of animals in the other group is simply $(1 - \pi)$, and the two groups have different capture probabilities that are also estimated. The notation $\pi(\cdot)$ indicates that the same mixing parameter applies to all 10 primary periods, whereas $\pi(t)$ indicates a different mixing parameter for each primary sampling period. Absence of a π parameter indicates a model without heterogeneity of capture probabilities.

There are two potential kinds of capture probabilities indicating the probability of capture in any secondary sampling period: those for initial captures (p , applied to

animals not previously caught in the primary period) and those for recaptures (c , applied to animals previously caught in the primary period). Initial capture probability was modeled as a single parameter for all primary periods, $p(\cdot)$, as a different parameter for each primary period, $p(t)$, or with two-group heterogeneity, $p(g)$. Based on results of closed-model analyses, we considered no models with time-specific capture probability over secondary periods.

Recapture probability, c , was modeled as a constant over all primary periods, $c(\cdot)$, as time dependent, $c(t)$, or with two-group heterogeneity, $c(g)$. The case in which two-group heterogeneity involves the same groups for both initial captures and recaptures is denoted as $p(g)$, [$c(g) = p(g) + C$]. We also considered models with time-dependent capture probabilities that included a relationship between initial and recapture probability. For example, the notation, $p(t)$, [$c(t) = p(t) + C$], indicates an additive relationship on the logit scale between time-specific capture and recapture probabilities. The model denoted as $p(t)$, [$c(t, g) = p(t) + C + g$] indicates time-specific variation in initial capture probability, and recapture probability varying in parallel (on a logit scale) with initial capture probability, but also including two-group heterogeneity. For models with no trap response (capture probabilities do not depend on previous capture history), the parameter p is used and there is no parameter c .

These different parameters and corresponding sources of variation led to set of 30 models that we considered to be most reasonable. We used AIC_c to select the most appropriate model for the data, a model that described the variation in the data well, yet without more parameters than necessary for adequate description (Burnham and Anderson 2002). We used the small-sample modification suggested by Hurvich and Tsai (1989). We did not use a quasi-likelihood adjustment because of the reasonable fit of the Cormack-Jolly-Seber (CJS) model to the data. This goodness-of-fit test deals only with the open portion of the likelihood (Williams et al. 2002), but we viewed this as the critical portion, given the great flexibility of the models for the closed portion of the likelihood. The difference between the AIC_c value for a given model and that of the low- AIC_c model is ΔAIC_c . The ΔAIC_c values are then used to compute model likelihoods and AIC_c weights. Model likelihoods reflect the relative strength of evidence for a particular model. Model weights can be viewed as the weight of evidence for a particular model being the "best" model for the data, conditional on the model set (see Burnham and Anderson 2002). If multiple models appeared to be appropriate (multiple models with relatively high AIC_c weights), then we intended to use model averaging (Buckland et al. 1997, Burnham and Anderson 2002) to compute estimates of parameters of interest.

We also computed other quantities of interest from parameters estimated by the modeling. The number of recruits was estimated by subtracting the expected

number of survivors from the previous period from the current population size (Pollock 1982, Williams et al. 2002). Under the standard open-population models, this is accomplished by subtracting the product of estimated abundance and survival, both for sample period t , from the estimated abundance at $t + 1$ (e.g., Pollock 1982, Seber 1982, Williams et al. 2002). However, the tiger data required a transient model with two different survival rates, one for newly caught animals (S'_t) and another for animals that were caught before the primary period (S_t). Thus, we estimated the number of new recruits in period $t + 1$ (B_t , animals present at $t + 1$ but not present in the population in any previous primary sampling period) as

$$\hat{B}_t = \hat{N}_{t+1} - \frac{\hat{N}_t[u_t(\hat{S}'_t)^{\Delta t} + m_t(\hat{S}_t)^{\Delta t}]}{u_t + m_t} \tag{1}$$

where u_t and m_t are the numbers of “unmarked” (not previously caught) and “marked” (previously caught) animals, respectively, at time t . These statistics are used to compute a weighted mean survival rate, where the weights correspond to the fraction of the population that is unmarked and marked, and the survival rates correspond to these two groups. The survival estimates are expressed as annual rates, and the Δt in expression (1) corresponds to the time interval (expressed in years) separating primary sampling periods t and $t + 1$. Variances of the recruitment estimates (Eq. 1) were obtained via parametric bootstrap. Under this procedure, data were simulated based on model estimates, simulated data were fit to the model, and estimates of recruitment were computed for each iteration from estimates of abundance and survival and the statistics for numbers of caught and uncaught animals. A variance of these recruitment estimates was computed directly.

We estimated the finite rate of increase (λ_t) or rate of change in abundance between sampling periods t and $t + 1$ as

$$\hat{\lambda}_t = \frac{\hat{N}_{t+1}}{\hat{N}_t} \tag{2}$$

There frequently is interest in the average rate of change over a period of time, sometimes referred to as “trend.” Thus, we also computed the geometric mean annual rate of increase of the $\hat{\lambda}_t$ as

$$\hat{\tilde{\lambda}} = \left(\prod_{t=6}^9 \hat{\lambda}_t\right)^{1/4.083} = \left(\frac{\hat{N}_{10}}{\hat{N}_6}\right)^{0.245} \tag{3}$$

where 4.083 is the number of years between primary sample periods 6 and 10, the period over which study area size was constant, and thus the period for which population change was estimated. Variances for these estimated rates of population change were estimated using delta method approximations (Seber 1982, Williams et al. 2002).

The derived parameters of expressions 1–3 all involve abundance estimates. In cases where temporary emigration is present, as with these data (see *Results*), there are two views of abundance. We can consider either the number of animals exposed to sampling efforts in a given primary period (the abundance, N_t , which is directly estimated), or the so-called superpopulation size, N_t^0 (see Kendall et al. 1997), which also includes animals that are temporary emigrants during the primary period. The two quantities are related by the probability of temporary emigration. In the case of random temporary emigration, the relationship is $E(N_t) = (1 - \gamma_t)N_t^0$, where γ_t is the probability that an individual in the superpopulation at period t is a temporary emigrant. Because both N_t and γ_t are estimated, it is possible to estimate superpopulation size as well, although this estimation requires untestable assumptions about the recruitment of new animals into the temporary emigrant component of the population at each sampling occasion. Here we have chosen to focus on the animals actually exposed to sampling efforts at each period, N_t , and our estimates of rate of change in abundance (Eqs. 2 and 3) and of recruitment (Eq. 1) apply to this group of animals.

As we have noted, our reason for not computing the rate of population change for the first years of the study was the two increases in size of the study area. These caused increases in the number of tigers exposed to sampling efforts and thus increases in abundance estimates. An alternative approach to estimating population change is to base the change on estimates of population density, \hat{D}_t , where density is defined as the number of tigers per unit area. This approach suffers from increased variances because of uncertainties associated with estimation of the area exposed to sampling efforts (Nichols and Karanth 2002), but it offers the advantage of providing estimates of rate of change in density that should not be affected by changes in the size of the study area. Thus, we estimated annual density and its variance using information about the area trapped and the maximum distances moved by individual tigers recaptured within seasons (Karanth and Nichols 1998, Nichols and Karanth 2002). We then obtained density-based estimates of population change as

$$\hat{\lambda}_t^D = \frac{\hat{D}_{t+1}}{\hat{D}_t} \tag{4}$$

The geometric mean of the nine resulting $\hat{\lambda}_t^D$ values was then computed as

$$\hat{\tilde{\lambda}}^D = \left(\prod_{t=1}^9 \hat{\lambda}_t^D\right)^{1/9.0} = \left(\frac{\hat{D}_{10}}{\hat{D}_1}\right)^{0.111} \tag{5}$$

Variances were again computed using delta method approximations (Seber 1982, Williams et al. 2002).

Although the density-based approach to estimation of population change greatly reduces the likelihood of

TABLE 2. Tests for population closure and model selection statistics based on tiger photographic capture history data from Nagarahole, India, 1991–2000.

Primary period	No. secondary periods	Mid-point	Closure test z	Closure test P	Model score			
					M_0	M_h	M_{bh}	M_{tbb}
1	6	May 1991	-0.60	0.27	1.00	0.94	0.95	0.90
2	5	Dec 1991	-1.00	0.16	1.00	0.81	0.65	0.64
3	3	Apr 1992	-0.71	0.24	1.00	0.98	0.63	0.73
4	7	Jan 1994	-0.68	0.25	1.00	0.89	0.62	0.70
5	10	Jan 1995	-1.04	0.15	0.72	0.71	1.00	0.90
6	18	Mar 1996	-0.89	0.19	1.00	0.75	0.63	0.68
7	8	Jun 1997	-1.16	0.12	1.00	0.93	0.56	0.62
8	12	Jan 1998	2.00	0.98	1.00	0.82	0.69	0.74
9	15	Mar 1999	-1.19	0.12	1.00	0.96	0.66	0.73
10	15	May 2000	0.94	0.83	0.90	0.80	1.00	0.99

Notes: Analyses were performed using program CAPTURE (Rexstad and Burnham 1991) separately for the secondary sampling periods within each primary period. The closure test z statistic is approximately distributed as normal (0, 1) under the null hypothesis of population closure. Model selection scores from the discriminant function (Otis et al. 1978) are reported for the four top-ranking models; higher scores indicate a more likely model. The models are: M_0 , constant capture probability; M_h , capture probability heterogeneous among individuals; M_{bh} , behavioral response in capture probability with heterogeneity among individuals; and M_{tbb} , capture probability affected by secondary sampling period, trap response, and heterogeneity.

estimates that reflect changes in sampling effects as well as changes in abundance, the approach may not entirely eliminate such effects. As is common in field studies of animal populations, the initial Nagarahole study area did not represent a random selection from the entire reserve, but was believed to have been the very best area for tigers and their prey. Expansion of this initial study area added areas that probably had slightly lower tiger densities than the original area. Thus, there might be a small tendency for rates of change in densities to reflect declines over time, especially for the two years in which area expansions occurred.

We followed the outlined density-based approach to estimation of population change because we wanted to draw inferences about population change for as many study years as possible. In terms of camera-trapping methodology, we suspect that others may experience similar changes in study area size and that our approach may prove useful in such cases. However, we note that our approach to estimating the area exposed to sampling efforts (required for density estimation), based on distances between recaptures of tigers (e.g., Wilson and Anderson 1985, Karanth and Nichols 1998), is ad hoc and not very satisfactory. We can envision better approaches based on radiotelemetry data, but expect such data to be relatively rare. As a result of these considerations, we have more faith in estimates of rate of population change based on abundance (Eqs. 2 and 3) than on density-based estimates (Eqs. 4 and 5).

RESULTS

Closure test results from program CAPTURE (Rexstad and Burnham 1991) using the secondary-period data from each of the 10 primary periods provided some evidence of gains and losses within primary periods (Table 2). Eight of the 10 closure test

statistics were negative, indicating possible lack of closure. We computed a composite z statistic as $Z = (\sum_{t=1}^{10} z_t) / \sqrt{10} = -1.37$, $P = 0.09$. This marginally significant test statistic provided some evidence of violation of the closure assumption. However, in the absence of strong evidence of lack of closure, we decided to view the sampled populations as approximately closed over the secondary periods of each primary period, permitting us to consider flexible models for detection probability.

Among the top four models receiving the highest model selection scores based on the CAPTURE algorithm for model selection, the constant-parameter model, M_0 , was selected for most data sets. However, it is known that this model is not robust to violation of underlying assumptions, and it generally is not used for modeling tiger populations (Nichols and Karanth 2002). We recognized that the full 10-period data set would provide more ability to discriminate among competing models and would be more likely to include other sources of variation. There was some evidence from the single-season CAPTURE analyses that heterogeneity and behavioral response were important, with less evidence of time (secondary period) effects. This exercise caused us to consider full models with heterogeneity, behavioral response, and time variation across primary periods, with only time variation across secondary periods excluded from our model set.

The goodness-of-fit test statistic from program RELEASE (Burnham et al. 1987) indicated an adequate fit of the Cormack-Jolly-Seber model to the data ($\chi^2_{16} = 16.11$, $P = 0.45$). However, biological reasoning caused us to look specifically at TEST 3.SR; its results were marginal, but provided weak evidence of a transient response ($\chi^2_8 = 11.69$, $P = 0.17$). Model selection based

TABLE 3. Model selection statistics for robust design analysis of tiger capture data from Nagarhole, India, 1991–2000.

Model description	AIC _c	ΔAIC _c	AIC _c weight	Model likelihood	No. parameters	Deviance
{S(a), γ''(.) = γ'(.), π(t), p(g), [c(g) = p(g) + C], N(t)}	1196.62	0.00	0.68	1.00	20	1156.86
{S(a), γ''(.) = γ'(.), π(.), p(t.), [c(t, g) = p(t) + C + g], N(t)}	1198.99	2.37	0.21	0.31	24	1149.84
{S(a + t), γ''(.) = γ'(.), π(.), p(t.), [c(t, g) = p(t) + C + g], N(t)}	1202.10	5.48	0.04	0.06	30	1138.34
{S(t), γ''(.) = γ'(.), π(.), p(t.), [c(t, g) = p(t) + C + g], N(t)}	1202.33	5.71	0.04	0.06	28	1143.51
{S(a), γ''(.) = γ'(.), p(t.), [c(t) = p(t) + C], N(t)}	1203.28	6.66	0.02	0.04	22	1158.86
{S(a), γ''(.) = γ'(.), π(t), p(h), c(h), N(t)}	1208.27	11.65	<0.01	<0.01	25	1156.73
{S(a), γ''(.) = γ'(.), π(.), p(t.), c(g), N(t)}	1210.13	13.51	<0.01	<0.01	24	1160.98
{S(a), γ''(t) = γ'(t), π(.), p(t.), [c(t, g) = p(t) + C + g], N(t)}	1211.19	14.57	<0.01	<0.01	30	1147.43
{S(a), γ''(.) = γ'(.), π(.), p(.), c(g), N(t)}	1212.65	16.03	<0.01	<0.01	17	1179.75
{S(a), π(.), p(.), c(g), N(t)}	1213.24	16.62	<0.01	<0.01	16	1182.59
{S(a), γ''(.) = γ'(.), π(t), p(.), c(g), N(t)}	1214.23	17.61	<0.01	<0.01	26	1160.29
{S(.), π(.), p(g), c(g), N(t)}	1214.88	18.26	<0.01	<0.01	16	1184.23
{S(a), γ''(.) = γ'(.), p(t.), N(t)}	1215.84	19.22	<0.01	<0.01	23	1169.06
{S(.), γ''(.), γ'(.), π(.), p(g), c(g), N(t)}	1216.42	19.80	<0.01	<0.01	18	1181.25
{S(a), γ''(.), γ'(.), π(.), p(.), c(g), N(t)}	1216.76	20.14	<0.01	<0.01	18	1181.59
{S(a), γ''(.) = γ'(.), p(t.), c(t), N(t)}	1216.85	20.23	<0.01	<0.01	31	1150.59
{S(a), γ''(.), γ'(.), π(.), p(g), c(g), N(t)}	1217.06	20.44	<0.01	<0.01	19	1179.60
{S(a), γ''(.) = γ'(.), π(.), p(t + g) = c(t + g), N(t)}	1217.67	21.05	<0.01	<0.01	25	1166.13
{S(a), γ''(.) = γ'(.), p(.), c(t), N(t)}	1218.51	21.89	<0.01	<0.01	24	1169.36
{S(.), γ''(.) = γ'(.), π(.), p(g), N(t)}	1219.62	23.00	<0.01	<0.01	15	1191.21
{S(a), γ''(.) = γ'(.), π(.), p(g), N(t)}	1220.74	24.12	<0.01	<0.01	16	1190.09
{S(a), γ''(.), γ'(.), π(.), p(g), N(t)}	1222.18	25.56	<0.01	<0.01	17	1189.27
{S(a), γ''(.) = γ'(.), p(t.), c(.), N(t)}	1223.35	26.73	<0.01	<0.01	22	1178.93
{S(a), γ''(.) = γ'(.), π(.), p(.), c(.), N(t)}	1226.12	29.50	<0.01	<0.01	15	1197.70
{S(a), γ''(.), γ'(.), π(.), p(.), c(.), N(t)}	1227.28	30.66	<0.01	<0.01	16	1196.63
{S(a), γ''(.) = γ'(.), π(t), p(g), c(.), N(t)}	1229.07	32.45	<0.01	<0.01	24	1179.92
{S(a), γ''(.) = γ'(.), π(.), p(g), c(.), N(t)}	1229.27	32.65	<0.01	<0.01	17	1196.36
{S(.), γ''(.), γ'(.), p(.), N(t)}	1231.68	35.06	<0.01	<0.01	14	1205.49
{S(a), γ''(.), γ'(.), p(.), N(t)}	1232.53	35.91	<0.01	<0.01	15	1204.11
{S(a), γ''(.) = γ'(.), π(.), p(t, g), N(t)}	1234.91	38.29	<0.01	<0.01	32	1166.13

Notes: Survival, S, is modeled as differing between the first (transient effect) interval following release vs. all subsequent intervals, but otherwise constant over time (a); as differing between the first (transient effect) interval following release vs. all subsequent intervals and varying in parallel over time (a + t); as differing between the first (transient effect) interval following release (constant value over time) vs. all subsequent intervals (time varying) (.t); and as constant over interval (no transient effect) and time (.). Probability of temporary emigration (γ) is modeled as random (non-Markovian) and constant over time [γ''(.) = γ'(.)]; as random (non-Markovian) and time varying [γ''(t) = γ'(t)]; as 0 (absence of γ notation); and as Markovian and constant over time [γ''(.), γ'(.)]. Probability of initial (p) and subsequent (c) capture within a primary period is modeled with two-group heterogeneity that is constant over time [π(.)]; two-group heterogeneity that is time varying [π(t)]; and no heterogeneity (absence of π notation). “(g)” indicates the capture probability to which heterogeneity applies (p or c). For example, “[p(g), c(g)]” indicates a two-group heterogeneity for both initial and recapture probabilities, but no relationship between the groups for the two kinds of capture probabilities; and “(p(g), [c(g) = p(g) + C])” indicates a two-group heterogeneity with the same groups for capture and recapture probabilities (C indicates that the group-specific probabilities differ for the two kinds of captures). A “(t.)” indicates time variation over primary periods but not secondary periods, whereas “p(t.), c(t) = p(t) + C]” indicates parallel time-specific variation for both capture and recapture probabilities. Both heterogeneity and time are sometimes modeled. For example “p(t.), [c(t, g) = p(t) + C + g]” indicates only time variation with no heterogeneity of capture probability, but parallel group-specific (heterogeneity) variation in recapture probability. Absence of “c” indicates equal capture and recapture probabilities; e.g., “p(t, g)” indicates time specificity and heterogeneity, but no distinction between capture and recapture probabilities. Population size is always modeled as time specific across primary periods, N(t).

on analyses using program TMSURVIV (Pradel et al. 1997) also indicated a need to consider transient models.

Model selection statistics for the full robust-design likelihoods (Table 3) provide inferences about relevant sources of variation in the parameters. The model with the lowest AIC_c is judged to be substantially better than the others in the set of 30 models (AIC_c weight = 0.68; the AIC_c weight of the nearest competitor is 0.21). Thus, we based most inferences on this model and decided not to use model averaging for parameter estimates.

Model {S(a), γ''(.) = γ'(.), π(t), p(g), [c(g) = p(g) + C], N(t)} was the selected lowest AIC_c model. Under this model, heterogeneous capture probabilities were modeled using constant group-specific capture ($\hat{p} = 0.40 \pm 0.067$; $\hat{p} = 0.15 \pm 0.020$) and recapture ($\hat{c} = 0.26 \pm 0.048$;

$\hat{c} = 0.080 \pm 0.010$) probabilities (all values are estimated means ± SE), with the proportion of animals in each group changing over time, π_t. The estimates of group composition, $\hat{\pi}_t$, were approximately 0 or 1 in four of the 10 years, indicating no evidence of heterogeneity in some years. As described in *Methods*, the two-group mixture model (Pledger 2000) is simply a likelihood-based approach to dealing with heterogeneous capture probabilities among individuals. Group membership is not known for any particular animal, and the model is a simple approximation of a reality in which each individual has a different detection probability. This model and associated estimates suggest some degree of trap response behavior, with recapture probabilities being somewhat smaller than initial capture probabilities.

TABLE 4. Estimated survival, abundance, rate of change in abundance, $\hat{\lambda}_t$, and recruitment for primary sampling periods for the tiger population in Nagarahole, India, 1991–2000.

Primary period, t	Date	Interval (Δt) from t to $t + 1$ (yr)	Annual survival, \hat{S}	Interval survival, $\hat{S}^{\Delta t}$	Abundance, \hat{N}_t	Population growth rate, $\hat{\lambda}_t$	Recruitment, \hat{B}_t
1	May 1991	0.667	0.77 (0.051)	0.85 (0.040)	9 (0.0)
2	Dec 1991	1.333	0.77 (0.051)	0.72 (0.061)	7 (2.6)
3	Apr 1992	0.750	0.77 (0.051)	0.83 (0.043)	11 (5.5)
4	Jan 1994	0.917	0.77 (0.051)	0.80 (0.048)	21 (3.2)
5	Jan 1995	1.250	0.77 (0.051)	0.73 (0.059)	12 (0.0)
6	Mar 1996	1.167	0.77 (0.051)	0.75 (0.056)	27 (1.4)	0.76 (0.12)	3 (3.2)
7	Jun 1997	0.583	0.77 (0.051)	0.87 (0.037)	20 (3.2)	0.86 (0.15)	0 (3.0)
8	Jan 1998	1.250	0.77 (0.051)	0.73 (0.059)	17 (1.7)	1.35 (0.15)	11 (2.8)
9	Mar 1999	1.083	0.77 (0.051)	0.77 (0.051)	23 (1.7)	1.29 (0.11)	14 (2.9)
10	May 2000				30 (2.1)		

Notes: Values in parentheses are estimated standard errors. Ellipses indicate occasions for which estimates are not reported because they reflect changes in study area size, in addition to true population changes. Blank cells (for May 2000) indicate quantities that were not estimable because the study ended as the sample year was beginning.

The equality of the two temporary emigration parameters indicated random temporary emigration, rather than Markovian (Kendall et al. 1997), with an estimate of $\hat{\gamma}'' = \hat{\gamma}' = 0.10 \pm 0.069$ ($\sim 10\%$ temporary emigrants in each primary period \pm SE). Estimates for tiger population dynamics parameters generated by the selected model are reported in Table 4. When scaled to an annual basis, the survival rates between primary sampling periods (\hat{S}_t) were estimated at 0.77 ± 0.051 . The survival estimates for newly caught animals, \hat{S}'_t , were used to estimate the probability that a new animal is a transient as 0.18 ± 0.11 .

Recruitment, abundance, and population rate of increase were computed for primary periods 6–10, the periods for which the study area remained unchanged in size. Recruitment estimates (\hat{B}_t) for these sample periods varied between 0 and 14, but these estimates were relatively imprecise (Table 4). Estimates of time-specific abundance (\hat{N}_t) ranged between 7 and 21 for the initial five primary periods, but because of changing sampled area size, these estimates are of little interest. Abundance estimates for primary periods 6 through 10, when the sampled area was held constant at 231.8 km², ranged

from 17 to 30 (Table 4), yielding estimated rates of population change ranging from 0.76 to 1.35, with relatively large variances, as expected for time-specific rates of increase. These are not annual estimates, but correspond to varying time intervals between successive sampling periods (Table 1). On an annual basis, the geometric mean rate of population change was estimated as $\hat{\lambda} = 1.03 \pm 0.020$ (estimated mean \pm SE), representing an approximate 3% annual increase between 1996 and 2000.

We also computed density estimates for all sampling periods, from 1991 to 2000, and computed corresponding rates of change in population density, $\hat{\lambda}_t^D$ (Table 5). Initial estimates of density and rate of change were very imprecise, reflecting the smaller numbers of animals sampled and the need to estimate the sampled area. Point estimates of λ based on density estimates and abundance estimates were virtually identical for the period 1996–2000. The density-based estimates had slightly lower precision, as expected, because of the uncertainty associated with estimation of the sampled area. The geometric mean annual rate of change from 1991 through 2000 and associated standard error are $\hat{\lambda}^D$

TABLE 5. Estimated abundance, area sampled by camera traps, population density, \hat{D}_t , and rate of change in density for primary sampling periods, for the tiger population in Nagarahole, India, 1991–2000.

Primary period, t	Date	Interval (Δt) from t to $t + 1$ (yr)	Abundance, \hat{N}_t	Sampled area, \hat{A}	Density, \hat{D}_t	Density change, $\hat{\lambda}_t^D$
1	May 1991	0.667	9 (0.0)	41.4 (3.3)	21.73 (1.7)	0.78 (0.30)
2	Dec 1991	1.333	7 (2.6)	41.4 (3.3)	16.91 (2.6)	0.64 (0.40)
3	Apr 1992	0.750	11 (5.5)	101.5 (5.2)	10.84 (5.4)	1.91 (1.01)
4	Jan 1994	0.917	21 (3.2)	101.5 (5.2)	20.69 (3.3)	0.57 (0.10)
5	Jan 1995	1.250	12 (0.0)	101.5 (5.2)	11.82 (0.6)	0.99 (0.08)
6	Mar 1996	1.167	27 (1.4)	231.8 (7.8)	11.65 (0.7)	0.74 (0.13)
7	Jun 1997	0.583	20 (3.2)	231.8 (7.8)	8.62 (1.4)	0.85 (0.17)
8	Jan 1998	1.250	17 (1.7)	231.8 (7.8)	7.33 (0.8)	1.35 (0.18)
9	Mar 1999	1.083	23 (1.7)	231.8 (7.8)	9.92 (0.8)	1.30 (0.15)
10	May 2000		30 (2.1)	231.8 (7.8)	12.94 (1.0)	

Notes: Values in parentheses are estimated standard errors. Blank cells (for May 2000) indicate quantities that were not estimable because the study ended as the sample year was beginning.



PLATE 1. Tigress with cubs. Multi-year camera trapping studies under robust design permit estimation of hard-to-obtain population parameters such as mortality and recruitment in tiger populations. Photo credit: U. Karanth/WCS.

$= 0.95 \pm 0.037$. As previously noted, this apparent decline in mean density is likely to be an artifact because the areas sampled in periods 1–5 had higher tiger densities than the expanded study area.

DISCUSSION

Modeling capture probabilities

Before we examine different aspects of tiger movement and demography, the modeling of capture probability merits discussion. Wege et al. (2004) have provided some evidence of trap shyness for tigers in Bardia reserve, Nepal. However, such trap response is not a universal characteristic of tiger photo-capture data, because we have found little evidence for it in other data sets obtained throughout India (Karanth and Nichols 1998, Karanth et al. 2004). More importantly, although we provide some evidence of trap response for Nagarhole tigers, we show that such trap response can be modeled under the robust design and presents no problems in terms of parameter estimation (i.e., it does not produce biased estimates).

Modeling tiger population dynamics

Traditionally, long-term studies of tigers based on either radiotelemetry or visual identification of individuals (Sunquist 1981, Smith 1993, Smith et al. 1999) have

classified tigers in a population as “residents” (breeding adults that defend stable home ranges), pre-dispersal offspring (cubs and juveniles), and “transients” (post-dispersal animals that are not “residents”). Such categorization of residents and transients is subjective and is based on the detection histories themselves. The probability of individual tigers not being detected despite their presence during some seasons is not considered in such post hoc classifications. On the other hand, many of our models were parameterized specifically to deal with transience (see Pradel et al. 1997), and model selection results provided strong support for these models. This “transient” parameterization does not necessarily correspond to what tiger biologists (Sunquist 1981, Smith 1993, Karanth and Sunquist 2000) term as “transience.” Our model specifies that transients are tigers caught for the first time that have virtually no chance of being captured again (estimated in this study as 18% of the tigers). These transients do not reside in the study area, but are viewed as individuals that pass through it once, while possibly trying to become residents elsewhere.

Our model also identified that a percentage of the tigers in the sampled population are “temporary emigrants,” individuals that may not be in the sampled area during some primary periods, although they are still in the superpopulation. Random temporary emi-

gration (Kendall et al. 1997) was required in our model, with an estimated probability of 0.10. Thus, about 10% of the tigers in the sampled area from year to year were estimated to be unavailable for being photo-captured (e.g., were located outside of the sampled area) during each primary sampling period.

Our model estimated the overall annual survival rate for tigers at 77%. The complement of this annual survival estimate is 23%, which includes deaths and permanent emigration out of the study area. Although the bulk of this annual loss of tigers is likely to be from mortalities, it also includes an unknown fraction of animals that permanently emigrate out of the area as dispersing subadults or as evicted residents (Smith 1993, Smith et al. 1999). Karanth and Stith (1999) hypothesized that although tiger populations have high mortality rates from natural and anthropogenic causes, they can be demographically viable if supported on an abundant prey base. In Nagarahole, between 1996 and 2000, despite an annual loss of 23%, overall recruitment was substantial, unlike in Russia (Kerley et al. 2003). Consequently, tiger numbers (Table 4) did not decline. Tiger densities were at high levels ranging between 7.3 and 21.7 tigers/100 km² over the nine-year period. The high prey density of ~56 ungulates/km² in Nagarahole (Karanth et al. 2004) appears to be critical for sustaining the pattern of tiger population dynamics that we observed (see Plate 1). Thus, our results support the specific prediction of a healthy tiger population in Nagarahole, as well as the general assumptions and predictions of the demographic model of Karanth and Stith (1999) that wild tiger populations can be demographically viable if supported by an abundant prey base, in spite of high rates of direct mortality.

Our results are consistent with our belief that unless the issue of maintaining high prey densities is addressed directly through improved reserve management, the current conservation focus on curbing the trade in tiger body parts may not be sufficient to assist species recovery across the tiger range.

Application of photographic capture-recapture sampling for elusive species

Our study was constrained by the limited number of camera traps we could deploy, particularly in primary periods 1–5. We believe that the precision of these parameter estimates can be improved by deploying more camera traps over a larger area and at higher densities, thereby capturing more individuals and increasing recapture rates. Also if the area increases to sample a greater proportion of the superpopulation, then the proportion of “temporary emigrants” may be reduced. We are testing these ideas in our ongoing studies. Despite some limitations, this study generated capture history data for 74 individual tigers and produced estimates of demographic parameters that are extremely difficult to obtain in wide-ranging, scarce, and elusive carnivore species.

Tiger abundance in Nagarahole fluctuated from year to year and estimates have relatively wide variances (Table 4). This is because our model explicitly incorporated uncertainties arising from factors related to tiger ecology as well as sampling issues. We believe that tiger monitoring programs that claim to be able to improve “precision” and “ability to detect changes” by essentially ignoring these uncertainties do not offer a valid alternative. Here we demonstrate that multiyear trend estimates for change in tiger population size ($\hat{\lambda}$) can be obtained with reasonable precision using models that deal satisfactorily with various ecological and sampling-related uncertainties. We believe that this efficient, noninvasive sampling approach is relevant to understanding the population dynamics of many other elusive or rare species in which individuals can be unmistakably identified from photographs or through other means.

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